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Diet of albacore (*Thunnus alalunga*) and yellowfin tuna (*Thunnus albacares*) off the south-west coast of South Africa

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Abstract

Considering the magnitude of albacore and yellowfin biomass, these two economically vital tuna species apply a considerable amount of predation pressure on prey communities off the South African coast. Nevertheless, little is known about their respective diets in this upwelling region. Fish Aggregating Devices (FADs), otherwise used globally, are banned in South Africa therefore giving us a unique opportunity to examine the natural diet of the tuna surrounding our shores. Sixty-one stomachs were sampled from recreational fishing competitions in May 2016 and 2018 off the south-west coast of South Africa to investigate the diets of albacore and yellowfin tuna. The fork length (mm) and wet weight (g) of the fish were recorded. The importance of each prey in the diet was estimated by the Index of Relative Importance (IRI). Each sample specimen was cut open, had its entire stomach carefully removed and frozen for later dissection and analysis. Prey items were initially grouped into fish, cephalopods and crustaceans and later identified to the lowest possible taxonomic level, counted, and weighed. The difference in diet between the species was investigated and modelled by Analysis of Similarity (ANOSIM), Non-Metric Multidimensional Scale (NMDS) and Principal Component Analysis (PCA). The feeding strategy was determined by Costello's Diagram. The 43 albacore and 18 yellowfin tunas ranged in fork length from 740 to 959 mm and 803 to 1720 mm, respectively. The most important prey class based on IRI in the diet of albacore was crustaceans (6162.01), followed by cephalopods (3672.47). For yellowfin the highest IRI was cephalopods (6269.39) followed by fish (3977.53) and unlike the diets of yellowfin in other parts of the world, crustaceans were numerically a very low prey item making up just 15.84% of the diet. Yellowfin, the larger of the two tuna species consume larger prey items and are more opportunistic than albacore, showing a greater vertical feeding range, by diving deep for cephalopods and surface feeding on offal from hake trawlers. Intra-species variations for both tuna proved to be smaller than the difference between the two species, with no substantial changes in either diet based on fish size. Unlike diets of tuna species in other parts of the world, the data suggest that southern African albacore and yellowfin were less dependent on fish (possibly due to the lack of FADs in the case of yellowfin), but more likely due to the higher availability of crustaceans and cephalopods at the upwelling front. The magnitude of the role of cephalopods in the Benguela ecosystem is likely to be underestimated.

Declaration

This dissertation is the result of my own research work. The contributions involved are acknowledged and referenced using the Harvard style. Other than assistance from my supervisors, I received no additional assistance, other than what has been acknowledged.

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Literature Review

Introduction

There are fifteen species of tuna widely distributed across the world's oceans. Belonging to the tribe Thunnini, tuna can be separated into five genera which comprise a monophyletic clade of the family Scombridae (Graham and Dickson, 2004). Tuna inhabit cold waters as far as latitudes 50°S and 60°N as well as the tropical waters in between, and account for a major proportion of global fishery production (Collette and Nauen, 1983). In South Africa, tuna are managed by a Total Allowable Effort (TAE) strategy, and thus instead of limiting the amount of catch, a restriction has been placed on the number of rights-holders allowed to catch tuna. There are two commercial fishing sectors which target tuna in South Africa, the Tuna Pole-Line (baitboat) and the Large Pelagic Longline sectors. As of 2019, 165 vessels held Tuna Pole-Line rights and 60 rights-holders hold 15-year long-term longline rights active since 2015 (IOTC, 2020).

Tuna catches are managed by regional fisheries management organizations (RFMO) and the total allowable catches (TACs) are distributed among member nations. These RFMOs are; International Commission for the Conservation of Atlantic Tuna (ICCAT), the Indian Ocean Tuna Commission (IOTC), and the Commission for the Conservation of Southern bluefin Tuna (CCSBT). Despite South Africa receiving a substantial TAC, the tuna quotas in the country remain underutilised. The value of the tuna available in its waters is close to one billion ZAR, and so it is within the best interest of the country to make full use of the quota. Albacore and yellowfin are the largest contributors to the South African tuna industry by both weight and number.

Thunnus alalunga, commonly known as albacore tuna, are found throughout the world's oceans, but are generally regarded as a temperate species. It is a highly migratory oceanic fish with specimens tagged off the east coast of the United States being later caught 8500 km away in Japanese waters (Molteno and Riley, 1986). As they get older their migrations cease and fish greater than 90 cm in length are mostly found in tropical and subtropical waters. Adult albacore do not exceed 120 cm in length. Albacore are able to inhabit waters of varying temperatures. Pacific longliners have located large concentrations in deep waters with temperatures as low as 7°C (Molteno and Riley, 1986). Surface schools, however, commonly range in waters between 16° and 20°C. The Atlantic Ocean is home to a northern and southern stock of albacore with little interchange between the two stocks (Molteno and Riley, 1986).

Albacore are the chief target for the South African tuna pole (bait boat) fleet which operates in waters up to 1000 km off the south and west coast of South Africa and Namibia. Caught by surface and longline gear, the South African albacore catch is the second largest in the region with annual landings of approximately 5000 t (West et al., 2014). South African albacore landings on tuna pole are caught only in the months of October to March when the tuna occupy coastal waters. They migrate north during summer which allows good catches in south Namibia between December and March. During the austral winter albacore will be targeted by longliners as they move offshore and away from pole boats. The stock status of albacore in both the Indian and Atlantic is optimal, as are the fishing pressures in the two regions. In 2018, tuna catch in local waters totalled approximately 2740 t (DEFF, 2020).

Yellowfin tuna (*Thunnus albacares*) are warm water apex marine predators which occupy tropical and subtropical pelagic waters (Pecoraro et al., 2017). The surface schools of younger yellowfin often mix with skipjack and bigeye tuna while the older fish tend to swim deeper and are abundant in tropical waters. Yellowfin tuna do not exceed 190 cm in length and a mass of 160 kg, with pole fishing or polling being their chief means of capture (Molteno and Riley, 1986). In South African Atlantic waters, yellowfin are predominantly found in the south-western Cape region from spring to summer. During the austral winter, they migrate far south, which affects the catches and the seasonality of the tuna pole fishery. Based on data up to 2017, the yellowfin stock is determined to be overfished, which can be attributed to the relatively low recruitment levels estimated in the years 2013 to 2015 (DEFF, 2020). In 2018 yellowfin landings totalled approximately 660 t (DEFF, 2020).

Bigeye tuna (*Thunnus obesus*) are commonly mistaken for yellowfin. Usually caught with yellowfin, bigeye is an offshore warm water species found in the Atlantic, Pacific and Indian Oceans. Longliners target large adults in deep water and the optimum sea surface temperature range is 18 to 20°C (Molteno and Riley, 1986). In South Africa, it is caught alongside yellowfin by bait boats on the Agulhas Bank from 95 to 350 km out to sea during spring and summer. During December and March small quantities are caught beyond the continental shelf on the west coast of South Africa on the Vema and Tripp seamounts (Molteno and Riley, 1986). The average annual catch of bigeye in the Atlantic between 1974 and 1978 was 39000 t which made up just above 20% of the world's catch during that period. The annual catch of bigeye in South Africa between 1980 and 1983 averaged 232 t. Bigeye are landed mostly by tuna pole boats and longliners (Molteno and Riley, 1986). In 2018, bigeye landings totalled 445 t in South African waters (DEFF, 2020).

Southern bluefin tuna (*Thunnus maccoyii*) are found throughout the Atlantic, Pacific, and Indian Oceans in a region stretching between latitudes 30° and 50°S. The majority of southern bluefin catches are in the Indian Ocean off the Australian coast (Molteno and Riley, 1986). Southern bluefin tuna are opportunistic feeders which prey on a wide variety of fishes, cephalopods and crustaceans (Murphy, 1976). Southern bluefin is an example of mismanagement and is now in a state of rapid decline with the original stock estimated at 600 000 t. In the mid-80s the maximum sustainable yield was only 28 000 t and South Africa's TAC as of 2021 stands at just 455.3 t (CCSBT, 2021). Surface schools have rarely been observed and most are caught by longliners in the South Atlantic (Molteno and Riley, 1986). The annual Large Pelagic fishery catch in South Africa in 2019 was 63.9 t (IOTC, 2020).

Skipjack (*Katsuwonus pelamis*) are an oceanic and highly migratory species of tuna found in all tropical and sub-tropical seas including the Mediterranean. Forming large surface schools, skipjack seasonally enter various coastal waters and are of high importance to local fishermen. Unlike albacore and blue fin tuna, skipjack spawn over large areas of the Indian, Pacific and Atlantic Oceans and are found in warmer waters of 20 to 24°C. Caught mainly by purse seiners or live-bait fishing, skipjack were not common in the Cape, but numbers have grown plentiful on the Agulhas bank in recent years. In 2018, skipjack landings in South Africa totalled 1,5 t (DEFF, 2020).

Despite having rich tuna grounds and a diverse range of tuna species, the ecological significance of these fishes have never been described in South Africa. There has been much interest in the ecology of the upwelling system on South Africa's west coast and the Agulhas Bank, and models have been developed based on countless diet studies of demersal and pelagic fishes, but the role of tunas are poorly known (Shannon, 1987). Typically, the tuna swim outside coastal waters, generally defined by coastal fronts, beyond oceanic water with temperature ranges between 18°C and 28°C (Branch, 2018).

The growing global interest in ecologically-based approaches to fisheries management (Pikitch et al., 2004, Marasco et al., 2007) has led to a renewed emphasis on understanding pathways of biomass and energy flow in exploited ecosystems (Olson et al., 2014). To develop ecosystem approaches to fisheries management, it is imperative to factor in species interactions and the underlying ecosystem dynamics. Predation by tunas is an important cause of mortality in the ecosystem, and so estimating the ecosystem flux could be an important step towards a more holistic understanding of South African water (Allain, 2004). Apex predators in pelagic ecosystems may have key impacts in determining food web structure and ecosystem dynamics (Essington et al., 2002).

The use of Fish Aggregating Devices (FADs) has increased and has displayed both positive and negative effects, and are not allowed to be used in South African waters. FADs have increased the catches on fish aggregations but have also led to a greater risk of the over-fishing of some species, decreasing the overall health of tuna stocks, a reduction in free-school abundance, and increasing the catch of juveniles (Morgan, 2011; da Silva et al., 2019). Large yellowfin tuna associated with FADs have considerably more food in the stomachs than large yellowfin captured away from FADs (Yesaki, 1983). FADs are free-floating and used by purse seiners to target tropical tunas and have greatly increased this fishery's efficiency (Moreno et al., 2016). There is, however, great concern surrounding FAD fishing (which yields nearly half of the world catch of tropical tunas i.e., skipjack, yellowfin and bigeye), which stems from the uncertainties around their impacts on tuna stocks and on the pelagic ecosystem (Marsac et al., 2000; Leroy et al., 2013; Dagorn et al., 2013). In contrast, albacore are not frequently associated with FADs.

Feeding Habits

Tunas are large pelagic predators that represent a high biomass in open-sea ecosystems (Menard et al., 2006). Magnuson (1978) reported that by continuously swimming in schools tuna have increased their hunting success in open-sea ecosystems where their food sources are inconsistently distributed. Tunas are known to feed on schooling stocks of sardines, anchovies, mackerel and squid (Alonso et al., 2005). For tuna to feed on fast swimming epi-pelagic fish, like sardines or anchovies that form highly dense schools on the continental shelves, they must continuously track them (Menard and Marchal, 2003). There are two main feeding actions among tuna species: filter-feeding (passive feeding), usually employed at night and active hunting using visual and vibration detection of prey. Tuna do not always hunt individual prey but seek out schools of favoured targets and once a prey concentration of one target species has been detected, tuna can feed on this concentration until satiation (Menard and Marchal, 2003).

Both albacore and yellowfin tuna do most of their feeding during the daylight hours by hunting, while at night they do more filter-feed using gill rakers (Menard and Marchal, 2003). Filter-feeding tunas prey predominantly on micronekton organisms that are ubiquitous and have predictable, vertical migrating behaviour (Menard et al., 2006). Typically, deep-sea predators with high metabolic rates (Kitchell et al., 1978; Olson and Boggs, 1986), yellowfin roam above the thermocline, in the top 150 m of the ocean but occasionally dive to depths of 350 m (Block et al., 1997).

Stomach content analysis of albacore is not as well reported at yellowfin. Despite its size and swimming capabilities, albacore forage in deep water and appear to favour small-sized, often slow-moving prey. In addition to small cephalopods, other prey items found in the albacore diet includes small fishes, gelatinous planktonic animals and amphipods (Bello, 1999). The vertical behaviour of albacore is still mostly unknown due to the fragile nature of the swim bladder which makes it problematic to capture fish in a suitable condition to tag and track (Bard et al., 1998). Feeding habits of albacore collected in the North Pacific and the Atlantic Ocean show that this species hunts from epi- to upper mesopelagic waters, to a depth of 500 m (Clemens and Iselin 1962; Aloncle and Delaporte 1973; Bernard et al., 1985; Ortiz de Zarate, 1987; Laurs and Lynn, 1991; Nihira et al., 1992; Hassani et al., 1997; Bertrand et al., 2002; Watanabe et al., 2004; Pusineri et al., 2005, Consoli et al., 2008). McHugh (1952) reported that albacore specimens from the eastern Pacific fish were dominant, making up almost 50% of the total food volume, while squids were the most important food amongst invertebrates. Furthermore, they reported that the diets of albacore captured in the eastern Pacific and eastern Atlantic are remarkably similar in composition.

Following albacore collection in the north-east Pacific Ocean in 1968 and 1969, Pinkas et al. (1971) reported that fish made up 86.0% and 92.7%, of the diets by volume respectively. A study by Hassani et al. (1997) conducted a dietary report of various species in the north-east Atlantic including dolphins and albacore. Albacore captured in the presence of dolphins had different stomach content to those caught without, mainly due to feeding competition between the predatory species. Despite that, the overall diets of 84 albacore by number consisted mainly of fish followed by crustaceans. Fish were also the most frequently occurring followed by cephalopods.

The South Pacific Ocean analysis by Bertrand et al. (2002) reported that cephalopods made up most of the albacore diet by weight followed by fish and lastly crustaceans. Specimens collected in the central North Pacific by Watanabe et al. (2004) showed that albacore diet by weight mainly consisted of fishes, followed by cephalopods and lastly crustaceans. The study shows a rise in fish consumption by weight, particularly anchovies, from July to September (79.9% and 95.2%, respectively), whereas the main squid prey almost disappeared during this time, likely due to the northward migration of the squid to subarctic waters in the boreal summer. This pattern suggests an opportunistic nature of albacore hunting.

Pusineri et al. (2005) conducted a report of 51 non-empty stomachs collected in 1993 from subtropical Atlantic Ocean and found that 63.9% of the albacore diet by reconstituted mass composed of fish, 34.8% cephalopods and 1.3% crustaceans. Fish had both the highest percentage frequency (95.9%) and percentage number (85.5%) while by cephalopods were present in 30.6% of stomachs but made up just 2.1% of the total number of prey items. Albacore from the central Mediterranean reported that fishes made up 67.1% and 52.1% of weight and number, respectively, and cephalopods (approximately 12.7% and 23.3%) and crustaceans (approximately 16.7% and 19.2%) (Consoli et al., 2008).

Tuna are known to form mixed schools consisting of skipjack, yellowfin and bluefin and being opportunistic predators are likely to have similar diets (Collette and Nauen, 1983). Yellowfin in the north-eastern Pacific Ocean have been recorded to have great vertical migrations to depths exceeding 1000 m (Shaefer et al., 2007). They are thought to feed predominantly during daylight and twilight hours while remaining primarily between the surface and 50 m at night (Alverson, 1963; Perrin et al., 1973, Shaefer et al., 2007).

Reintjes and King (1953) have summarized investigations preceding 1953 on the yellowfin feeding in the Central Pacific Ocean. Their findings and subsequent publications (King and Ikehara, 1956; Watanabe, 1958; Alverson, 1963; Allain, 2004; Menard et al., 2006; Rohit et al., 2010; Setyadji et al., 2012; Olson et al., 2014; da Silva et al., 2019) indicate that the predation of the yellowfin throughout the world's oceans is opportunistic and take advantage of whatever is most plentiful in the area at the time (Reintjes and King, 1953; Perrin et al., 1973; Collete and Nauen, 1983; Roger, 1994; Shin and Cury, 2004; Menard et al., 2006; Jaquemet et al., 2011). These findings mean that the diets of yellowfin should provide an excellent indication of what resources are present in the areas where they feed. Shannon (1987) further highlighted the opportunistic feeding nature of yellowfin in that they have been observed feeding extensively on hake offal on the western edge of the Agulhas Bank.

The specimens for the study by Reintjes and King, (1953) were captured in the central Pacific using various fishing methods, originated from different habitats, and were of varying sizes. Of the total volume of the stomachs, contents contained 47% fish, 26% squid, and 25% crustaceans. Crustaceans were by far the most frequently occurring and highest numerically, particularly crab larvae (megalopa) in the 1097 samples. Based on the timing of capture, with fish caught in the afternoon by trolling and live-bait fishing had greater quantities of food in their stomachs and fewer empty stomachs than those caught in the morning. They assumed that feeding must take place during daylight hours. The yellowfin caught at the surface had been feeding primarily on crustacean larvae and fish, while tuna caught beneath the surface on fish and squid. They discovered that smaller yellowfin predominantly consumed crustacean larvae; medium-sized yellowfin fed on fish, crustacean larvae, and squid; while the larger fish fed mainly on fish and squid. Furthermore, of the 38 families of fish and 10 orders of invertebrates in the yellowfin stomachs, only seven families of fish and three orders of invertebrates provided more than 2% of the total food volume studied.

Studies by Ronquillo (1953) and Watanabe (1958) recorded similar diets to the Reintjes and King (1953) study for yellowfin captured in the Western Pacific and Indian Oceans, respectively. Unlike Reintjes and King (1953), they recorded the total number of times an item appeared in the stomach, rather than the volume. Despite this, Ronquillo reported that only six families of fish and two orders of invertebrates of the 36 families of fish and seven orders of invertebrates recorded, were the greatest contributors to the diet. Watanabe's findings showed that only seven families of fish and two orders of invertebrates of the total 37 families of fish and eight orders of invertebrates noted, covered the greatest portion of the food consumed. They recorded that fish had the highest Index of Relative Importance (IRI), followed by cephalopods, and crustaceans almost negligible. Alverson, (1963) reported the diets of 3,763 yellowfin tuna, caught in various areas of the eastern Pacific, by volume comprised mainly of fish (47%), followed by crustaceans (45%), then cephalopods (8%). Crustaceans, particularly red and swimming crabs, were the most frequently occurring prey group in the study appearing in 76% of stomachs, followed by fish (54%) and cephalopods (33%).

Stomach samples from 611 yellowfin tuna captured by live bait, longline, trolling, and purse seine in three regions of the Atlantic Ocean were collected in 1965 and 1966 (Dragovich, 1972). All three areas of collection, eastern and western tropical Atlantic and the subtropical Atlantic Ocean showed that fish, by volume, was the highest contributor with size of the forage items primarily based on displacement volumes. Fish and crustaceans prey items were respectively most frequently occurring and numerous. Cephalopods, despite significantly being the least numerous (approximately 12%) prey item made up a large portion of the diet by volume (approximately 35%).

A yellowfin study conducted by Buckley and Miller (1994) found that pre-FAD, non-FAD- and FAD-associated diets showed some differences in the South Pacific in terms of frequency, number and weight. Comparisons of respective non-FAD and FAD-associated diets showed crustaceans were consistently the most frequently occurring (92.02% and 90.5%) while a significant increase in the number from 795 to 1424, with shrimp jumping from 42 to 591. With the use of FADs the importance of fish increased rather considerably in both occurrence (68.8% to 85.3%) and weight (77.5% to 91.8%). Crustaceans were the most frequently occurring with Bertrand et al. (2002) reporting that the diet of yellowfin tuna are composed mainly of prey present in the shallower layers and feed significantly on the juveniles of reef fishes when available. Of the three zones of study in the South Pacific Ocean, fish were found to be the dominant prey item by weight followed by cephalopods. In the central Pacific, 95 FAD associated and 74 non-FAD-associated yellowfin were collected (Brock, 1985). Opposing the findings of Buckley and Miller (1994) yellowfin caught in areas removed from FADs, fish went from the most consumed food item from 66% to 15% by volume and frequency of occurrence dropped from 48% to 22%. Crustaceans went from 28% by volume in non-FAD areas to 85% of volume in

FAD-associated-areas.

A study of yellowfin and bigeye tuna in western tropical Indian Ocean was conducted by Potier et al. (2004). Prey items were processed by occurrence, number, and wet weight and it is reported that of the 110 longline yellowfin samples gathered that crustaceans made up 81.4%, with crab larvae making up 66.8%, of the percentage number. Hard parts were counted but weights were not reconstituted. The study further described that tuna diets have shown a shift in prey from fish to crustaceans in recent years which may have lowered the trophic level of these top predators. All the prey groups showed a high percentage occurrence in the stomachs with fish at 81.8%, cephalopods at 75.5% and crustaceans at 70.9%. A study of species including 111 Yellowfin was conducted in the western equatorial Indian Ocean by Potier et al. (2007). Percentage frequency of occurrence showed that fish was present in 82.0% of samples, cephalopods at 85.6% and crustaceans at 71.2% of which crab larvae were an important prey item.

Menard et al. (2006) examined 97 yellowfin caught in the French Polynesian Exclusive Economic Zone (EEZ) in the central Pacific Ocean, by longline fishing. Using classification by weight, the overall yellowfin stomach's contents approximately contained 60% fish, 35% squid and 5% crustaceans. A trend also emerged in that as the yellowfin grow larger than 90 cm their feeding on fish increases and the feeding on both crustaceans and squid decrease. da Silva et al. (2019) investigated 212 yellowfin samples collected in the western equatorial Atlantic Ocean. Their IRI values from the diet of specimens indicate that fish, particularly flying fish and lantern fish, are the main prey of yellowfin. Cephalopods were both higher in number and occurrence than crustaceans with *Brachyuran megalopae* showing a high contribution in number.

Dissanayake et al. (2008) analyzed yellowfin samples collected in the eastern Indian Ocean. Twelve families were identified in the stomachs and of the three prey groups crustaceans were found to be the most abundant by number (58.77%) and have the highest percentage IRI (%IRI) of 50.73. *Charybdis smithii* of the family Portunidae was by far the most important prey item with a %IRI of 49.48. Fish were found to be the greatest by weight (48.18%) and a %IRI of 38.29, while %IRI of cephalopods was 10.98.

Rohit et al. (2010) analused 146 Non-empty yellowfin specimens from the north-eastern part of the Indian Ocean and used IRI and prey specific abundance to characterise diets. By mass, fish was the most dominant prey item (52.9%) followed by crustaceans (27.3%) and cephalopods (19.3%). The most dominant prey item occurrence was fish (65.1%), and crustaceans by number (47.2%). Numerically, crustaceans, including the *Brachyuran megalopae*, were the most abundant prey at

47.2% and had an IRI of 35.7%, while fish had the highest IRI (47.07%).

South Africa is one of the few countries that do not allow FAD fishing in its waters. The diets of fish captured here should be unaffected by FADs. Studies of tuna feeding habits in various oceans have been reported but few studies have been conducted in the South Atlantic, and none in South African waters. This study uses stomach content analyses to provide regionally comparative quantitative and qualitative analysis of the stomach contents of albacore tuna and yellowfin tuna collected from fishing vessels off the south-west coast of South Africa. Data from these analyses may be used to make inferences about fish feeding behaviour and trophic conditions and coupled with the opportunistic nature of tuna feeding and the composition of prey items available in the region.

Methods

A total of 61 stomachs (43 albacore and 18 yellowfin) were obtained from fish caught 40 nautical miles south west of Cape Point (Fig. 1). The fish were caught during recreational fishing competitions in May 2016 (40 albacore and eight yellowfin) and May 2018 (three albacore and 11 yellowfin). The fork length (mm) and wet weight (g) of the fishes were recorded. Each fish was cut open and the entire stomach carefully removed, stored in airtight packets and frozen for later dissection and analysis.

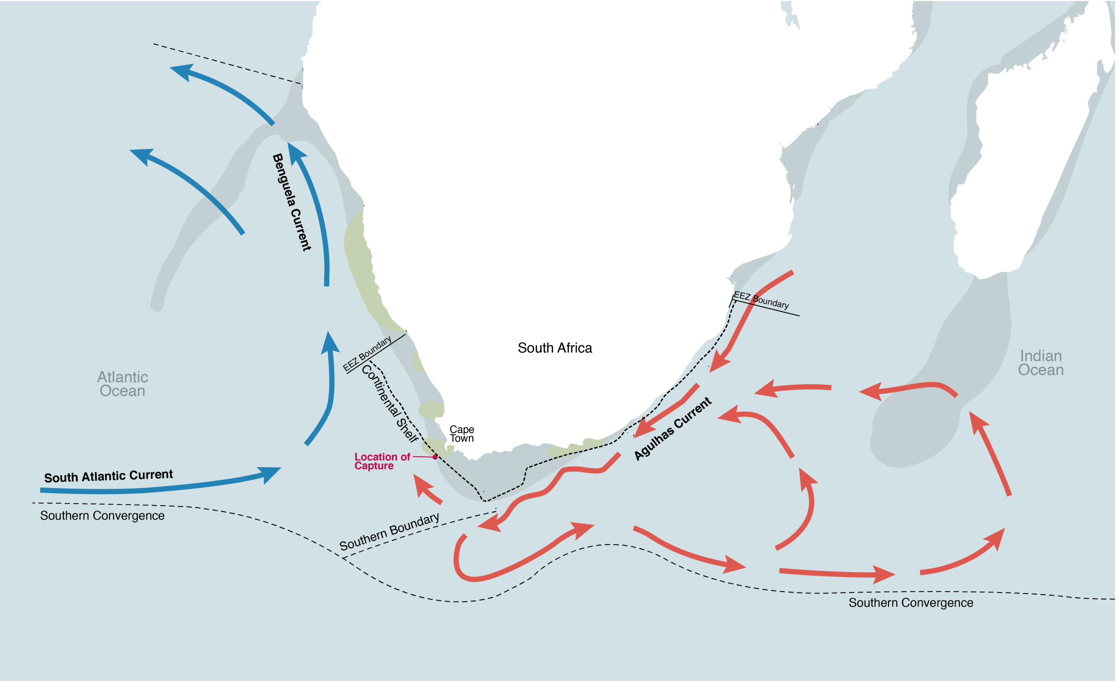

Figure 1: Map of southern African showing the location of capture of the 61 specimens caught during recreational fishing competitions in May of 2016 and 2018

The stomachs were removed from storage and thawed completely. Each stomach was weighed (to the nearest 0.1 g). Each stomach was cut open and all the contents were removed and weighed. A 1 mm sieve was used to drain the liquid contents. The stomachs were rinsed with water and any remaining solids were caught in the sieve.

Prey items were grouped according to their taxa. The prey in each taxon were then weighed to the nearest 0.1 g. The digestion status of each prey item was recorded according to Table 1. All prey items were identified to the lowest possible taxonomic level, counted, and weighed. Keys and descriptions that were used for identification included Monod (1968), Clarke (1986), Crosnier and Forest (1973), Smith and Heemstra, Eds. (1991) and Smale et al. (1995). Prey items were measured for the standard length for fish, mantle length for cephalopods, and cephalothorax, telson length and total length for crustaceans. To identify partly digested prey items, the hard parts (fish otoliths and cephalopod beaks) were photographed using a dissecting microscope. Hard parts are resistant to digestion and may accumulate in the stomachs over a greater period of time. The lengths of the hard parts were recorded for species identification and to approximate a reconstituted weight. Cephalopods and fish that bodies were digested and were up to digestions status of 6 and 7 respectively were reconstituted as the weights of these prey items were an untrue reflection of the actual weight. For cephalopods regression equations from Clarke (1986) were used to calculate the weight from the lower rostral length (LRL). Images of the otoliths were also captured and compared using Smale (1995), Campana (2004) and Kristoffersen (2007), the last of which provided otolith length to weight conversions.

Table 1: Digestion states of the respective prey categories

Status	**Fish**	**Cephalopods**	**Crustaceans**
1	Intact	Intact	Intact
2	Whole body, without skin	Whole body, without skin	Cephalothorax uplifted
3	Whole body, ruptured visceral cavities but entire dorsal spine (or broken but can be reconstituted)	Suction cups absent, damaged mantle (non measurable)	Cephalothorax and abdomen apart
4	Head, body and organs apart	No more mantle, mouth intact	Flesh being digested
5	Skull, dorsal spine, free jaws tied on	Mouth bulb with beak, mouth tore up, dispersed "plumes"	Cephalothorax cuticles empty and scattered
6	Skull with otoliths, free jaws tied on, intestines	Beaks intact	Eyes with base of antennas
7	Non eroded free otoliths, intact jaws	Beaks free and eroded	
8	Otoliths and big bones eroded	Beaks free and broken	

Index of relative importance

The digestion state of each prey item was recorded and an average is shown in Table 2. The dietary importance of each prey type was calculated by methods based on frequency of occurrence, number and weight (Buckland et al., 2017). Each prey item's contribution to tuna diet was determined by three relative measures of prey quantity (Hyslop 1980): Relative frequency of occurrence of each food item (%F); the proportion in the number of each item in the total stomach content (%N); and the proportion in weight of each item in the total stomach content (W%). These percentages refer to all stomachs, empty or non-empty. The overall importance of each prey item was estimated using the Index of Relative Importance (IRI) proposed by Pinkas et al. (1971), and converted to percentage weight:

$$\mathrm{IRI} = (\%\mathrm{N} + \%\mathrm{W}) \times \%\mathrm{F} \tag{1}$$

Costello's diagram

Costello's diagram was used to determine the feeding strategy (Costello, 1990; Amundsen et al., 1996). This graphic method consists of a scatter plot composed of each prey-specific abundance (P) relative to its occurrence, and is calculated by the formula:

$$\mathrm{P} = \frac{\sum SA}{\sum StA} \times 100 \tag{2}$$

where P is prey specific abundance; SA is the sum of prey A in number or weight and StA is the sum of total prey, in number or weight only in the stomachs where prey A was found (Costello, 1990; Amundsen et al., 1996). Weight of prey was used for this study. Information about prey importance and feeding strategy of the predator is given by the distribution of the points relative to the diagonals and axes of the graph (da Silva et al., 2019).

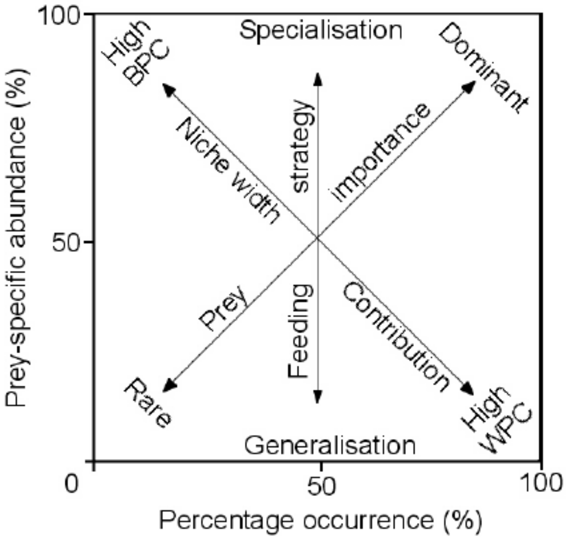

Figure 2: The Costello diagram (Amundsen et al., 1996) and its interpretation to indicating feeding strategy. (BPC = between-phenotype component; WPC = within-phenotype component)

Multivariate analysis

Of interest is the similarity (or dissimilarity) of the diets between the two species of tuna. To explore this, three techniques were used. The most direct technique used to test for a difference in diet between the two tuna species is Analysis of Similarities (ANOSIM). This technique provides a way to test statistically if there is greater variation in diet between the tuna species than within. Prior to performing the ANOSIM, the entries in the data were changed to proportions of diet instead of absolute counts. Four models were run, (i) a full model with the species; (ii) full model against the length categories; (iii) length categories of yellowfin only; (iv) length categories of albacore only.

To further explore the similarity, non-metric multidimensional scaling (NMDS) and principal component analysis (PCA) were used to visualise the similarities between fish in low dimensional space. While these techniques both reduce the dimensionality of a dataset, the approaches to reducing dimensions are very different. NMDS aims to represent high-dimensional data in low dimensional space using rank orders. PCA, on the other hand, attempts to decompose the data into k principal components. Furthermore, NMDS and PCA do different things - NMDS clusters similar samples based on abundance of different variables whereas PCA identifies the contributions of the different variables to the orthogonal axes as a means of reducing dimensions in the data set and grouping similar variables. PCA was used because the loadings (how each variable load onto the principal components) are interpretable.

Regression models determine and quantify the effects of variables on some other response variable. The species of tuna can be predicted, based on the prey items found in the stomach. The logistic regression model uses a binary response variable (species of tuna) with predictor variables that are the abundances of each prey type (equation 3 shown below).

$$log(\frac{p}{1-p}) = \beta_0 + \beta_1 X_1 + \cdots + \beta_n X_n + e \tag{3}$$

where $p =$ the probability of the fish being of a particular species, β_i are the regression coefficients, X_i is the count of prey item n.

The logistic regression model is useful in determining which factors are significant in classifying observations into the respective groups (in this case, albacore or yellowfin). Initially, the full data set was used (21 prey items and 1 response variable). However, the standard errors of coefficients were large when including all 21 explanatory variables. There were too few observations (too little information) to estimate the 21 regression coefficients. It was, therefore, decided to use the lower dimensional approximation of the dataset obtained through PCA and NMDS. In this way, there are only three explanatory variables (the three dimensions/components) that were used to classify an observation into a species group. In the logistic regression model, X_{is} are the associated values for each prey item in each dimension/component.

Results

The fork length ranged between 740 to 959 mm and from 803 to 1720 mm for yellowfin and albacore, respectively. The average fork length for albacore was 834.97 ± 48.29 mm (n = 43) and the average fork length for yellowfin was 1382.57 ± 246.23 mm (n = 18).

Stomach content analyses

Albacore

Only two albacore stomachs were empty. In the remaining 41 stomachs a total of 463 prey items were found in the albacore diet. After reconstituting the weight of items represented by hard parts only, the total weight increased from 0.94 kg to 1.25 kg. Each fish averaged 11.29 prey items per stomach. Of the three classes, crustaceans occurred most frequently at 85.37% (%F), followed by cephalopods and then fish (Table 2)). By number (%N), the diet also consisted mostly of crustaceans (52.05%), represented by 12 families, and five orders, followed by cephalopods (30.02%). By weight, cephalopods made the highest contribution to the total diet 41.68% (%W), followed by fish at 29.05%.

Overall, the main prey items in the albacore tuna diet were crustaceans (with an IRI of 6162.01), of which amphipoda and decapoda had the highest IRIs of 1493.90 and 1333.50, respectively. Oegopsida was the most important order across all three prey classes with an IRI of 2929.60. The Brachioteuthidae was the dominant family, with an IRI of 1308.99 and of the four cephalopod species identified, *Brachioteuthis* sp. had the highest IRI of 379.86. Five species of fish were identified, all of which were Myctophidae belonging to four different genera, with *Symbolophorus boops* having the highest IRI of 86.42.

Yellowfin

There were no empty yellowfin stomachs. 101 prey items were found in the yellowfin diet. After reconstituting the weight of items represented by hard parts only, the total weight increased from 3.27 kg to 16.43 kg. Each fish averaged 5.32 prey items per stomach.

Of the three classes, fish occurred most frequently at 66.67 (%F), followed by cephalopods and then crustaceans (Table 2). By number (%N), the diet also consisted mostly of cephalopods (49.51%), represented by two orders, followed by fish (23.76%). By weight, cephalopods made the highest contribution to the total diet 63.34% (%W), followed by fish at 35.89%.

Overall, the main prey items in the yellowfin tuna diet were cephalopods (with an IRI of 6269.39), of which octopoda had the highest IRI of 2087.39. Oegopsida was the most important order across all three prey groups with an IRI of 2929.60. The Brachioteuthidae was the dominant family, with an IRI of 1308.99 and of the four cephalopod species identified, *Ornithoteuthis volatilis* had the highest IRI of 815.07. Two species of fish were identified, *Merluccius capensis* and *Scomber scombrus*, with the former having the higher IRI of 561.74.

Inter-species comparison

The inter-species comparison showed that cephalopods were common to both predators, while crustaceans included some common prey items. Fish, however, constituted the largest difference between the two species with no common prey item between them.

Mean digestion states in the two tuna species show that yellowfin prey items had higher mean digestion states for each of the three prey groups (Table 2). For cephalopods the mean of digestion state in albacore was 4.79 ± 1.75 and 5.90 ± 1.02 in yellowfin. For fish (4.12 ± 1.52 and 4.88 ± 0.89) and crustaceans (3.29 ± 1.09 and 4.63 ± 1.99) the mean digestion states were again higher for yellowfin. For every prey item common to the two species, yellowfin had a higher mean digestion state, often considerably.


[redacted]
[redacted]

Figure 3: Two images of the same otolith of the family Myctophidae from an *albacore* stomach photographed using a dissecting microscope

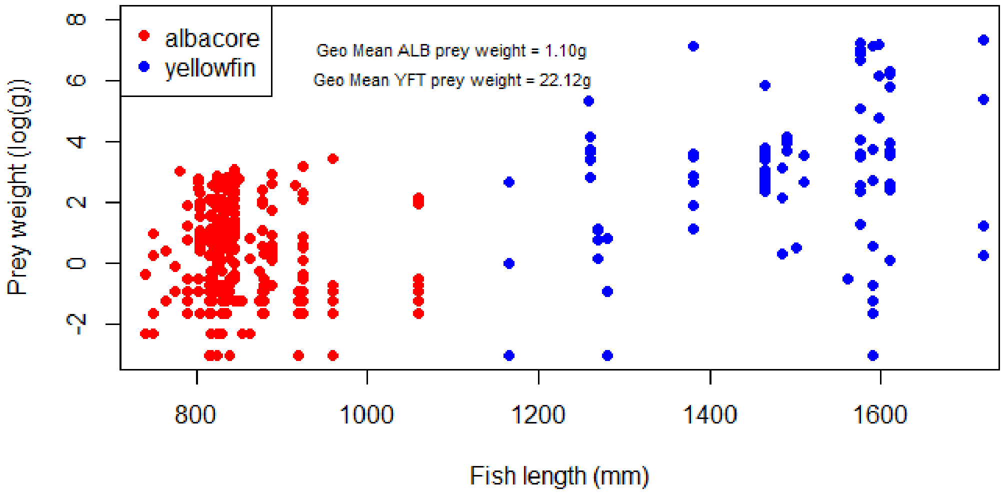

Figure 4: Plot of lengths of *albacore* (red) and *yellowfin* tuna (blue) vs weight of respective prey items on a natural log scale caught off the south-west coast of South Africa. The geometric mean is shown.

The scatter plots of log-transformed prey weights against fish length show a clear separation according to tuna species, but very much overlap between prey sizes. However, yellowfin prey attain weights of at least one order of magnitude greater than the prey of albacore. The geometric means of prey item reconstituted weight were 1.1 and 22.1 g for albacore and yellowfin respectively. (Fig. 4). Yellowfin displayed a greater prey-weight variation with a number of individual yellowfin tuna had prey-weight greater than 1 kg. There was no pattern in prey size across different size fish within each species.

Table 2: **Relative contribution by food item from number (%N), weight (%W) in grams, frequency of occurrence (%F), and Index of Relative Importance (IRI) from the diet of *albacore* and *yellowfin* tuna caught off the south-west coast of South Africa [Ce: Cephalopods; Cu: Crustaceans; Mean DS: Mean digestion state]**

	Albacore					**Yellowfin**				
Food item	N%	F%	W%	IRI	Mean DS	N%	F%	W%	IRI	Mean DS
Cephalopods	30.02	51.22	41.68	3672.47	4.79 ± 1.75	49.51	55.56	63.34	6269.39	5.90 ± 1.02
OCTOPODA	0.86	7.32	2.33	23.35	5.75 ± 0.5	19.8	27.78	55.35	2087.39	6.00 ± 0.00
Octopodidae						9.90	22.22	54.42	1429.19	6.00 ± 0.00
Opisthoteuthidae	0.22	2.44	1.77	4.86	6.00 ± 0.00	9.90	11.11	0.93	120.32	6.00 ± 0.00
Opisthoteuthis	0.22	2.44	1.77	4.86	6.00 ± 0.00	9.90	11.11	0.93	120.3	6.00 ± 0.00
Opisthoteuthis massyae	0.22	2.44	1.77	4.86	6.00 ± 0.00	9.90	11.11	0.93	120.3	6.00 ± 0.00
OEGOPSIDA	27.43	46.34	35.79	2929.61	4.61 ± 1.64	27.72	50.00	7.92	1782	5.68 ± 1.22
Brachioteuthidae	22.03	31.71	19.25	1308.99	4.81 ± 1.62					
Brachioteuthis	10.15	19.51	9.32	379.86	3.62 ± 1.62					
Brachioteuthis sp.	10.15	19.51	9.32	379.86	3.62 ± 1.63					
Lycoteuthidae	1.94	17.07	12.05	238.81	4.89 ± 1.69	3.96	5.56	0.85	26.75	6.00 ± 0.00
Lycoteuthis	1.94	17.07	12.05	238.81	4.89 ± 1.69	3.96	5.56	0.85	26.75	6.00 ± 0.00
Lycoteuthis lorigera	1.94	17.07	12.05	238.81	4.89 ± 1.69	3.96	5.56	0.85	26.75	6.00 ± 0.00
Ommastrephidae	3.46	7.32	4.50	58.27	3.13 ± 0.81	20.79	33.33	6.72	916.91	5.71 ± 1.10
Ommastrephes						0.99	5.56	2.07	17.00	6.00 ± 0.00
Ommastrephes bartrami						0.99	5.56	2.07	17.00	6.00 ± 0.00
Ornithoteuthis	0.22	2.44	1.32	3.76	2.00 ± 0.00	19.8	33.33	4.65	815.07	5.70 ± 1.13
Ornithoteuthis volatilis	0.22	2.44	1.32	3.76	2.00 ± 0.00	19.8	33.33	4.65	815.07	5.70 ± 1.13
Unidentified Squid	1.51	14.63	2.50	58.67		1.98	11.11	0.07	22.78	
Fish	12.31	41.46	29.05	1714.79	4.12 ± 1.52	23.76	66.67	35.89	3977.53	4.88 ± 0.89
CLUPEIFORMES						2.97	5.56	0.68	20.25	6.00 ± 0.00
Clupeidae						2.97	5.56	0.68	20.25	6.00 ± 0.00
GADIFORMES						4.95	16.67	28.75	561.78	4.40 ± 1.67
Merlucciidae						4.95	16.67	28.75	561.78	4.40 ± 1.67
Merluccius						4.95	16.67	28.75	561.74	4.40 ± 1.67
Merluccius capensis						4.95	16.67	28.75	561.74	4.40 ± 1.67
MYCTOPHIFORMES	8.42	26.83	23.63	859.9	3.51 ± 0.91					
Myctophidae	8.42	26.83	23.63	859.9	3.51 ± 0.91					
Diaphus	0.43	2.44	1.35	4.34	3.5 ± 0.71					
Diaphus effulgens	0.43	2.44	1.35	4.34	3.5 ± 0.71					
Lampichthys	0.22	2.44	0.47	1.68	6.00 ± 0.00					
Lampichthys procerus	0.22	2.44	0.47	1.68	6.00 ± 0.00					
Metelectrona	0.22	2.44	0.57	1.93	4.00 ± 0.00					
Metelectrona ventralis	0.22	2.44	0.57	1.93	4.00 ± 0.00					
Symbolophorus	4.54	9.76	16.87	208.96	3.14 ± 0.73					
Symbolophorus barnardi	0.86	4.88	2.84	18.06	2.25 ± 0.50					
Symbolophorus boops	3.67	4.88	14.04	86.42	3.35 ± 0.61					
SCOMBRIFORMES						5.94	22.22	2.11	178.87	2.67 ± 0.82
Scombridae						3.96	16.67	2.09	100.85	3.00 ± 0.82
Scomber						3.96	16.67	2.09	100.82	3.00 ± 0.82
Scomber scombrus						3.96	16.67	2.09	100.82	3.00 ± 0.82
Nomeidae						1.98	5.56	0.02	11.12	2.00 ± 0.00
STOMIIFORMES	0.22	2.44	0.56	1.76	2.00 ± 0.00					
Sternoptychidae	0.22	2.44	0.56	1.76	2.00 ± 0.00					
Maurolicus	0.22	2.44	0.56	1.76	2.00 ± 0.00					
Maurolicus muelleri	0.22	2.44	0.56	1.76	2.00 ± 0.00					
Unidentified fish	2.59	24.39	3.43	146.83		5.94	27.78	1.12	196.13	
Unidentified fish remains	0.22	2.44	0.01	0.56		3.96	22.22	3.23	159.76	

Table 2 (Continued)

	Albacore					**Yellowfin**				
Food item	N%	F%	W%	IRI	Mean DS	N%	F%	W%	IRI	Mean DS
Crustaceans	52.05	85.37	20.13	6162.01	3.29 ± 1.09	15.84	22.22	0.22	356.85	4.63 ± 1.99
AMPHIPODA	30.02	43.90	4.01	1493.92	3.03 ± 0.58	7.92	5.56	0.01	44.09	4.38 ± 0.74
Hyperiidae	30.02	43.90	4.01	1493.92	3.03 ± 0.58	7.92	5.56	0.01	44.09	4.38 ± 0.74
DECAPODA	12.31	58.54	10.47	1333.54	3.07 ± 0.92	0.99	5.56	0.09	6.00	4.00 ± 0.00
Acanthephyridae	1.51	9.76	0.72	21.76	3.28 ± 0.95					
Carcinidae	2.59	14.63	0.26	41.70	2.33 ± 0.65					
Penaeidae	6.48	36.59	9.27	576.29	3.27 ± 0.91	0.99	5.56	0.09	6.00	4.00 ± 0.00
Funchalia	1.73	12.2	5.65	90.04	3.00 ± 0.00					
EUPHAUSIACEA	0.65	7.32	0.12	5.64	2.67 ± 0.58	0.99	5.56	0.09	6.00	3.00 ± 0.00
Euphausiidae	0.65	7.32	0.12	5.64	2.67 ± 0.58	0.99	5.56	0.09	6.00	3.00 ± 0.00
MYSIDA	0.86	2.44	0.10	2.34	3.00 ± 0.00					
Mysidae	0.86	2.44	0.10	2.34	3.00 ± 0.00					
STOMATOPODA	4.97	21.95	1.88	150.36	3.65 ± 1.11					
Unidentified Cu	0.65	7.32	0.42	7.83		4.95	16.67	0.01	82.68	
Unidentified Cu remains	0.43	4.88	0.71	5.56		0.99	5.56	0.02	5.62	
Unidentified remains	5.62	63.41	9.14	935.93		10.89	61.11	0.55	699.1	

Table 3: The results of four ANOSIM of diets between (i) *albacore* and *yellowfin* tuna, (ii) among length classes regardless of species and (iii and iv) among length classes within each species.

Model	**R**	**Significance**
(i) Species (full)	0.221	0.001
(ii) Length (full)	0.187	0.010
(iii) Length (yellowfin)	0.085	0.250
(iv) Length (albacore)	0.035	0.324

The first ANOSIM model shows that the two tuna species have strongly divergent diets. The two models that test the effect of length within each species show that there is no length effect when the effect of species is removed Table 3.

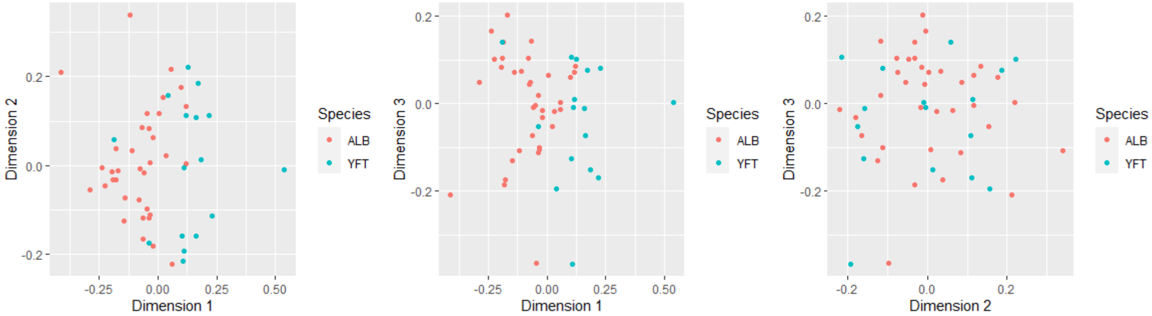

Figure 5: Plot of Non-Metric Multidimensional Scale (NMDS) in three dimensions from the diet of *albacore* (red) and *yellowfin* (blue) tuna caught off the south-west coast of South Africa [ALB = albacore; YFT = yellowfin]

Pairwise plots of the three dimensions extracted from the NMDS shows clear species separation the two of the three pairings that involve the first dimension (Fig. 5). It is clear the dimension 1 seems to be capturing most of difference between the species. Dimensions 2 and 3 offer very little differentiation.

Table 4: Table of logistic regression analysis of the Non-Metric Multidimensional Scale (NMDS) from the diet of *albacore* and *yellowfin* tuna caught off the south-west coast of South Africa.

Variable	**Estimate**	**Standard error**	**p-value**
(Intercept)	-1.621	0.516	0.001
Dimension 1	16.902	5.126	< 0.001
Dimension 2	-1.3423	2.301	0.559
Dimension 3	-5.207	3.296	0.114

The logistic regression of NDMS confirms what can be seen from the pairwise plots. Dimension 1 differentiates between the two species (Table 4). However, it is not possible to identify what difference this dimension captures.

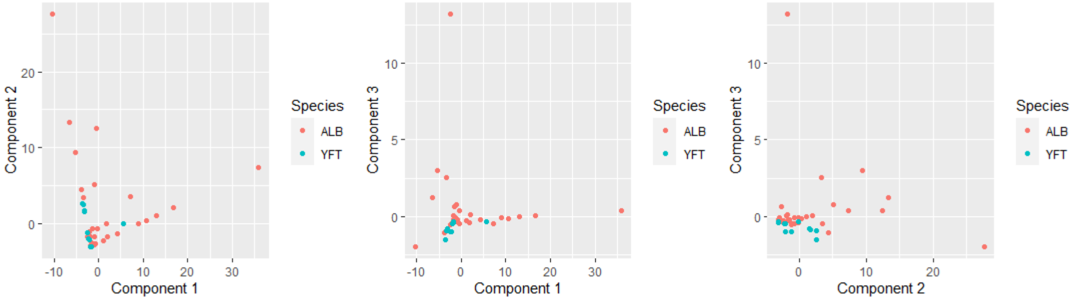

Figure 6: Plot of principal component analysis (PCA) from the diet of *albacore* tuna and *yellowfin* tuna caught off the south-west coast of South Africa

From the pairwise plots of the components obtained from PCA, it is seen that all three components differentiate the species in some way (Fig. 6). The PCA loadings below (Table 6) provide more specifics than NMDS, which show differentiation between the tuna species diets.

Table 5: Logistic regression: PCA of the diet of *albacore* and *yellowfin* tuna caught off the south-west coast of South Africa

Variable	**Estimate**	**Standard error**	**p-value**
(Intercept)	-42.087	17.793	0.018
Component 1	2.867	1.258	0.02
Component 2	-6.532	2.767	0.02
Component 3	-75.421	31.999	0.02

The logistic regression of PCA confirms what can be seen from the pairwise plots. The three components are significant in differentiating between the two species (Table 5).

In order to investigate what variance each component is capturing, the loadings of each prey item onto each component can be analysed. These loadings are summarised in Table 6 below.

Table 6: PCA loadings of the diet of *albacore* tuna and *yellowfin* tuna caught off the south-west coast of South Africa

Prey item	Component 1	Component 2	Component 3
Amphipoda	0.96	0.26	0.02
Clupeiformes	-0.00	-0.00	-0.01
Decapoda	0.11	0.04	0.03
Euphausiacea	-0.00	0.01	0.00
Gadiformes	-0.00	-0.01	-0.01
Myctophiformes	-0.07	0.20	0.43
Mysida	-0.00	-0.01	-0.00
Octopoda	-0.03	0.01	-0.08
Oegopsida	-0.26	0.94	-0.09
Scombriformes	-0.01	-0.01	-0.02
Stomatopoda	-0.02	0.07	0.13
Stomiiformes	-0.00	0.02	-0.01
Teuthida	-0.01	-0.02	0.88

The first component is associated with higher loading values for Amphipoda, Decapoda, and Oegopsida (loading values 0.96, 0.11, and -0.26 respectively) (Table 6). Interestingly, Amphipoda and Decapoda have positive loading values while Oegopsida has a negative loading. Amphipoda and Decapoda tend to be more prevalent in the diet of albacore relative to yellowfin and Oegopsida tends to be more prevalent in the diet of yellowfin (although this is not nearly as significant as the difference in eating patterns of Amphipoda and Decapoda). The greatest loading onto component 3 is associated with prey item Teuthida (loading value 0.88). Albacore tend to eat more Teuthida than yellowfin do (in fact, in this dataset, none of the yellowfin had Teuthida in their stomachs). Other prey items of interest are Stomatopoda (loading value 0.13) and Myctophiformes (loading value 0.43). Again, these prey items were not part of the diet of yellowfin, however, were present in the diet of albacore. Component 2 captures similar variance to that captured by components 1 and 3. The prey items holding the largest loading values onto component 2 are Oegopsida, Amphipoda, and Myctophiformes (loading values 0.94, 0.26 and 0.2 respectively).

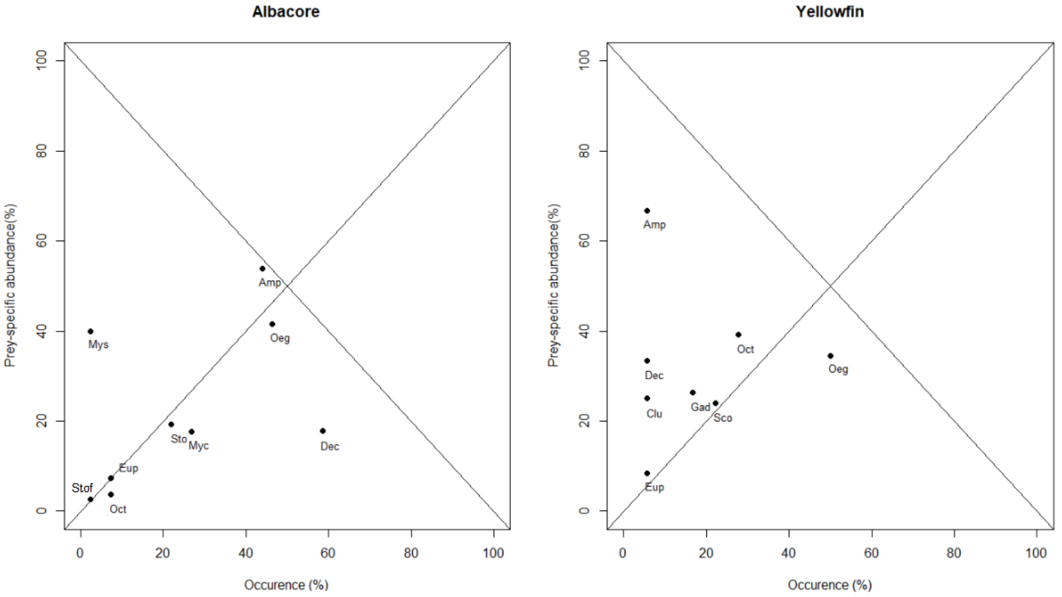

Figure 7: Costello's Diagram from the diet of *albacore* and *yellowfin* tuna caught off the south-west coast of South Africa. Amp, Amphipoda; Cep, Cephalopods; Cru, Crustaceans; Clu, Clupeiformes; Dec, Decapoda; Eup, Euphausiacea; Gad, Gadiformes; Myc, Myctophiformes; Mys, Mysida; Oeg, Oegopsida; Oct, Octopoda; Sco, Scombriformes; Stof, Stomiiformes; Sto, Stomatopoda

The Costello's Diagram (Fig. 7) shows that albacore and yellowfin demonstrate a High Between Phenotype Component (BPC), with varying degrees of specialization and generalization on different prey items. For yellowfin, most prey were located below the prey importance axis while most albacore prey were above this axis, thus indicating that albacore was exploiting a broader niche with a more generalised feeding behaviour than yellowfin. Both species, particularly yellowfin, exhibited a feeding specialisation on amphipods. Oegopsida was located in a similar location showing approximately a 50% occurrence and halfway along the importance axis.

Discussion

Considering the magnitude of albacore and yellowfin biomass, these tuna species apply a considerable amount of predation pressure on the epi- and mesopelagic communities off the South African coast. Tuna are opportunistic predators rather than selective feeders (Reintjes and King, 1953; Perrin et al., 1973; Collete and Nauen, 1983; Roger, 1994; Shin and Cury, 2004; Menard et al., 2006; Jaquemet et al., 2011) and the dominance of a few items in their diets should reflect the relative abundance in the ecosystem (Potier et al., 2004). Additionally, the specimens sampled in this study were not captured in a region that uses FADs which should give a natural indication as deployment of the devices may lead to changes to the feeding habits of various species in the region and thus alter the ecology of an area in that predation of prey groups may change.

Albacore

Despite its size and swimming capabilities, albacore appear to prefer smaller slower moving prey such as small cephalopods and small fishes, mainly myctophidae (Bello, 1999). In contrast, crustaceans proved to have the greatest IRI in South African albacore diets and thus indicating a lower trophic level nature of their feeding than suggested by Bello (1999). Myctophidae are known to conduct large, vertical migrations (Bertrand et al., 2002) and are found in mesopelagic waters while *Lycoteuthis lorigera*, Brachioteuthis and *Ornithoteuthis volatilis* are commonly located at these depths. These prey items, typically being the larger of the major contributors to the albacore diet, provide an insight to their daylight active feeding at mesopelagic depths. The high proportion of crustaceans in the diets of albacore indicate they commonly feed closer to shore in this upwelling region, but do not hunt as shallow as yellowfin. Albacore feed at the upwelling front.

The high importance on crustaceans and large input of weight by cephalopods shown in this study is dissimilar to data from other regions. Reports of albacore from the north- and north-east Pacific found that fish were the greatest contributor to their diets by volume and weight, respectively (Pinkas et al., 1971; Watanabe et al., 2004). Similar results were shown by Pusineri et al. (2005) in the subtropical Atlantic Ocean. Diets of central Mediterranean albacore was made up of fish by both weight and number, with crustaceans having the lowest numerical contribution of the three prey groups (Consoli et al., 2008). One study, however, did showcase some similarities to this study with diets of albacore in South Pacific being made up by weight mostly of cephalopods then fish and lastly crustaceans (Bertrand et al., 2002).

Yellowfin

Yellowfin have a diet typical of an oceanic species with cephalopods, oegopsida and octopoda, representing the main source of food, by numerical abundance, weight and importance. The dominance of cephalopods provides an indication of how rich this prey group is in the region. As there are no South African fisheries target octopods on the continental shelf or oceanic water, we have very little information to judge the abundance of species in this taxon. The diet of of yellowfin suggests that a large resource of octopods is available below the thermocline. It is quite likely that models of ecosystem structure have systematically ignored this group because of lack of information as such information is typically derived from fishing or fish surveys. Ecosystem modellers might need to take note of the possibility that octopods play a far greater role in the Benguela than previously estimated (Shannon, 2000). The diet composition shows the great depths at which the yellowfin can feed, especially considering the vertical migrations of cephalopods that dive deeper during the daylight hours in which tuna feed.

Similar to albacore, the yellowfin results from other parts of the world report that fish made up most of the diet by weight (Reintjes and King, 1953; Watanabe, 1958; Alverson, 1963; Menard et al., 2006; Dissanayake et al., 2008; Rohit et al., 2010). Little inter-annual and inter-seasonal variability was found. The inclusion of hard parts and subsequent reconstituted weights could have lead to an overestimation of the importance of prey items, yellowfin in particular, due to the resistant nature of these prey items (Battaglia et al., 2013).

However, Reintjes and King (1953) reported that crustaceans were the most abundant numerically as well the most frequently occurring in the central Pacific Ocean, which is unlike the findings of this study. Findings of studies conducted in the eastern Indian (Dissanayake et al., 2008) and north-eastern Indian Ocean (Rohit et al., 2010) reported that crustaceans were the greatest numerical contributor to albacore diets. Similarly, in the South Pacific Ocean crustaceans were the most frequently occurring (Bertrand et al., 2002). Yellowfin had little dietery preference for crustaceans, suggesting a lack of night time passive feeding which is a significant factor in the respective diets and feeding strategies of yellowfin tuna elsewhere (Buckley and Miller, 1994; Dragovich, 1970; Potier et al., 2004; Rohit et al., 2010).

Influence of FADs and availability of prey

The influence of FADs is a significant factor in the differences in the diet of tuna species around the world. The lack of use of FADs in southern African waters may explain why fish is not as important in yellowfin diets. Buckley and Miller (1994) compared pre-FAD, non-FAD- and FAD-associated diets. They found that the presence of fish in the diets of yellowfin increased with the use of FADs in the

South Pacific.

In contrast, albacore are not frequently associated with FADs. Samples from the subtropical Atlantic, central Mediterranean and both the north-, north-east Pacific have fish as the main dietery group by IRI (as discussed above). The South African albacore prefer crustaceans and cephalopods to fish, similar to yellowfin.

Both species, one which is known to be affected by FADs and the other not, show a preference for crustaceans and cephalopods in South Africa's FAD-free water. The dietery composition of these two species might simply reflect the greater availability of crustaceans and cephalopods in the region of the Bengeula upwelling front.

Inter-species comparison

There is a dissimilarity of the prey resources between yellowfin and albacore. The analysis of feeding habits of albacore showed crustaceans as the main source of food numerically and by occurrence, possibly in the region where there is a short food chain, as is the case in upwelling zones (Potier et al., 2004). It is also indicative of the feeding strategy of albacore in that they hunt more passively than yellowfin, which feed at a higher trophic level. The dissimilarities between the tuna diets likely occurred due to the variations in foraging range in the water column, or even by the differences in the size distributions of each species. Yellowfin show a greater vertical feeding range than albacore (Block et al., 1997; Bertrand et al., 2002; da Silva et al., 2018), along with the opportunistic behaviour that might vary in the region and areas of occurrence (Jaquemet et al., 2011; Menard et al., 2006).

Yellowfin, being the larger of the two species, consumed larger prey items such as squid and large fish. The most frequently occurring large fish is *Merluccius capensis* (Cape hake) which lives between 300 and 700 m depths during the day. This prey species is also primary target of the Hake trawl fishery which is active in the exact region where these tuna were caught. As tuna have frequently been seen scavenging off trawlers it would seem that fish component of the yellowfin diet has been elevated by the practice of scavenging (Shannon, 1987). The natural reliance of yellowfin on cephalopods, although high, has probably been underestimated. The other two groups of fishes found in yellowfin stomach are not frequently associated with the catches of bottom trawlers. *Scomber scombrus* (Atlantic Mackerel) is a smaller pelagic fish, more commonly associated with yellowfin diets and may therefore be considered a natural part of the yellowfin diet. The even smaller, Clupeidae, common inside of the upwelling front (i.e. not in the zone where yellowfin feed) were infrequently recorded.

Despite feeding on smaller prey items, albacore show a far more generalised feeding strategy than yellowfin tuna, consuming a greater variation of prey items. The fewer number of yellowfin stomachs analysed in the present study may explain such differences. There is no pattern in prey size across different size fish within each species. Yellowfin has higher digestion states when comparing common prey items between the two tuna species thus indicating lower feeding rates than albacore.

Conclusion

In contrast to other parts of the world, the two species examined here have an unusually high reliance on cephalopods and crustaceans. Tuna are likely to exert a major predation force on these groups outside of the Benguela upwelling front. Tuna are typically associated with waters above 16°C, i.e. on the oceanic side of the cold upwelled water. The effect of the lack of FADs only affects yellowfin as this gear-type is not used to catch albacore. Both tuna species show a similar difference in diet to those caught elsewhere, suggesting that it is the local availability of prey that sets their diet apart. Cephalopod biomass is likely to be far larger in this region than commonly known and the role of cephalopods, particularly squid, in the ecosystem outside of the upwelling front warrants further investigation.

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